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VIDEO EVIDENCE OF SIBLICEIDE AND CANNIBALISM, MOVEMENT OF NESTLINGS BY ADULTS, AND INTERACTIONS WITH PREDATORS IN NESTING HEN HARRIERS

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ABSTRACT.—During a nest-camera study of Hen Harriers (*Circus cyaneus*), we recorded siblicide, cannibalism, movement of nestlings by adult birds, and interactions with predators. We deployed cameras at 13 nests across three study areas in Ireland between 2008 and 2010. At a nest with two well-developed nestlings (approximately 25–30 d old), the older nestling killed its sibling and fed on it. This was the first documented case of siblicide in this species, to our knowledge. Recordings also revealed three other events of cannibalism in which one of the nestlings in a brood died from unknown causes and was then eaten by its siblings ($n = 1$), by the adult male ($n = 1$), or was used by the adult female to feed the remaining nestlings ($n = 1$). At two nests, recordings showed the adult female picking up and moving nestlings that were outside the nest cup. In addition, cameras recorded two instances of full brood predation by red fox (*Vulpes vulpes*) and an attack on a nest by a female Eurasian Kestrel (*Falco tinnunculus*) that had no apparent consequences for the nestlings or the female Hen Harrier. The behaviors reported here, which are difficult to observe directly, may have important consequences for our understanding of productivity and population dynamics of Hen Harriers.

KEY WORDS: *Hen Harrier*; *Circus cyaneus*; *cannibalism*; *nest camera*; *nest defense*; *nestling moving*; *siblicide*; *sibling aggression*.

EVIDENCIA EN VIDEO DE FRATRICIDIO Y CANIBALISMO, MOVIMIENTO DE POLLUELOS E INTERACCIONES CON DEPRADADORES EN NIDOS DE *CIRCUS CYANEUS*

RESÚMEN.—Durante un estudio sobre patrones de actividad de individuos reproductores de *Circus cyaneus* realizado con cámaras para monitoreo de nidos, registramos comportamientos de fraticidio, canibalismo, movimientos de polluelos e interacciones con depredadores. Colocamos cámaras en 13 nidos distribuidos en tres áreas de estudio en Irlanda entre 2008 y 2010. En un nido con dos polluelos en un estado de desarrollo avanzado (c. 25-30 días), el polluelo de mayor edad mató al otro y se alimentó de él. Este es el primer caso documentado de fraticidio en esta especie. Obtuvimos imágenes de otros tres casos de canibalismo en que uno o más polluelos fallecieron por causas desconocidas y sus cadáveres fueron usados como alimento por los otros polluelos ($n = 1$), por el macho adulto ($n = 1$) o por la hembra adulta para alimentar a los otros polluelos ($n = 1$). En dos nidos, las imágenes muestran a la hembra adulta repetidamente recogiendo polluelos que se alejan del nido para intentar llevarlos al nido. Por último, las cámaras captaron dos eventos de depredación de polluelos por parte de *Vulpes vulpes* y un enfrentamiento entre la hembra adulta de *C. cyaneus* y una hembra de *Falco tinnunculus* sin consecuencias para los polluelos o la hembra adulta. Estos comportamientos, difíciles de detectar mediante metodologías de monitoreo

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tradicionales, pueden tener consecuencias para el éxito reproductivo y la dinámica poblacional de esta especie.

[Traducción de los autores editada]

Hen Harriers (*Circus cyaneus*) are listed as an Annex-I species by the European Union Birds Directive (OJEU 2010), are a species of conservation concern, and are the focus of considerable research in Ireland and the United Kingdom due to ongoing population declines (Colhoun and Cummins 2013, Eaton et al. 2015). There are currently fewer than 157 breeding pairs of Hen Harriers in Ireland (Ruddock et al. 2016), and fewer than 545 territorial pairs in the UK (S. Wotton pers. comm.).

Hen Harriers are ground-nesting birds, and as such their eggs and nestlings are vulnerable to predation by terrestrial predators (Baines et al. 2008, Wilson et al. 2012, McMillan 2014). Nesting behavior and breeding ecology are therefore of particular interest due to their influence on nest predation rates, breeding success, and population dynamics. However, published information on Hen Harrier nesting behavior is limited to direct observations at nest sites in Scotland (Watson 1977, Amar et al. 2008, Leckie et al. 2008). Although remote cameras have made a significant contribution to ecological research since their development, and have been widely used as a tool to monitor different aspects of the ecology of nesting birds (Pietz and Granfors 2000, Smithers et al. 2005, Cox et al. 2012), they have rarely been used to study Hen Harriers.

As part of a long-term study investigating optimum scenarios for Hen Harrier conservation in Ireland (Irwin et al. 2012), we deployed nest cameras at sites across three study areas to research activity patterns at nests (Fernández-Bellón et al. 2017). Nest-camera recordings can also provide insight into infrequent behaviors or interactions that would be rarely observed or recorded by direct observations and other methods (Steen et al. 2016, Aguiar-Silva et al. 2017, Robinson et al. 2017). Here, we present evidence of previously unreported siblicide behavior at a Hen Harrier nest, and also document cases of cannibalism, movement of nestlings by adults, and interactions with predators.

METHODS

We monitored Hen Harrier nests at three study areas in the Ballyhoura Mountains (52°17.62' N 8°33.93' W, County Cork), West Clare Mountains (52°47.83' N 9°13.63' W, County Clare), and Slieve Aughty Mountains (53°02.91' N 8°35.86' W, County Galway) in Ireland during three consecutive breeding seasons (2008–2010). We used standard Hen Harrier survey protocols to search for nests (Hardey et al. 2013) and deemed nests suitable for camera deployment where this could be achieved without risk of attracting the attention of the public or of making access to the nest easier for terrestrial predators (e.g., by altering the

surrounding vegetation). At 13 nests, we deployed digital cameras during incubation, activated by motion detection via a passive infra-red sensor (MemoCam DV-Cop/CELL, Video Domain, Tel Aviv, Israel), yielding a total of 255 nest-recording days (see Fernández-Bellón et al. (2017) for further details on nest cameras).

We analyzed nest-camera recordings for behaviors of interest. We defined behaviors of interest for nestlings as any behavior other than resting or feeding on prey provisioned by adults, and we defined behaviors of interest for adults as any behavior other than incubation, brooding, and provisioning of nestlings. We report nest success rate as the percentage of nests with eggs that fledged at least one young, and productivity as the number of young fledged per successful nest (nests fledging at least one young). We conducted nest-camera deployments and associated fieldwork under license from the National Parks and Wildlife Service of Ireland

RESULTS

The success rate of nests with cameras was 76.9%, with an average productivity of 2.7 young fledging per successful nest (Table 1). Behaviors of interest recorded by cameras were siblicide ($n = 1$), cannibalism ($n = 4$), movement of nestlings by the adult female ($n = 2$), and interactions with predators ($n = 3$).

Siblicide and Cannibalism. We recorded four cases of cannibalism at four separate nests in this study (see Supplementary Material Video 1). At a nest in the Ballyhoura Mountains in 2010 (nest BM10b) cannibalism was preceded by siblicide, the first report of this behavior in Hen Harriers, to our knowledge. At the time of the event, the nest had two female young, age 25–30 d, both wing-tagged and banded. Both Hen Harrier nestlings were apparently healthy when the older bird attacked and killed its younger sibling (Fig. 1a). The older nestling proceeded to feed on its dead sibling over the next few days, mantling over it when the adult female landed at the nest.

At two other nests (nests SA10a and WC10b), we recorded cannibalism after the youngest nestling died from causes other than siblicide. At the nest in the Slieve Aughty Mountains in 2010 (nest SA10a), the youngest nestling of a brood of five hatched 10 d after the oldest, but died from unknown causes within 24 hr of hatching. The adult female proceeded to feed it to the remaining nestlings (Fig. 1b). At a nest in the West Clare Mountains in 2010 (nest WC10b), five nestlings hatched within 7 d of each other. The older nestlings occasionally exhibited aggression toward the youngest and that nestling died following a heavy rainstorm when the brood's age ranged

Table 1. Breeding parameters and behaviors of interest recorded at 13 Hen Harrier nests monitored by cameras from 2008 to 2010 in Ireland.

NEST ID	YEAR	STUDY AREA	NO. OF EGGS	NO. OF NESTLINGS HATCHED	NO. OF NESTLINGS SURVIVED	BEHAVIORS OF INTEREST RECORDED
BM08a	2008	Ballyhouras	5	3	3	-
BM08b	2008	Ballyhouras	na ^a	3	0	Cannibalism by male
BM08c	2008	Ballyhouras	5	4	0	Predation by red fox
SA08a	2008	Slieve Aughties	4	3	2	-
BM09a	2009	Ballyhouras	5	3	3	-
BM09b	2009	Ballyhouras	5	4	2	Interaction with Eurasian Kestrel
BM09c	2009	Ballyhouras	5	2	0	Predation by red fox
WC09a	2009	West Clare	4	3	2	-
BM10a	2010	Ballyhouras	5	4	3	-
BM10b	2010	Ballyhouras	4	2	1	Siblicide and cannibalism
SA10a	2010	Slieve Aughties	6	5	4	Cannibalism by female
WC10a	2010	West Clare	3	3	3	Movement of nestlings
WC10b	2010	West Clare	6	5	4	Cannibalism and movement of nestlings

^a Not available. Camera deployment at this nest was 3 d after hatching.

between 18–25 d old. One of the other nestlings then fed on it.

Finally, at a nest in the Ballyhoura Mountains in 2008 (nest BM08b), three apparently healthy nestlings approximately 24 d old died during the night due to unknown causes. On returning to the nest the following day, the adult male unsuccessfully attempted to carry away one of the nestlings. The adult male returned 3 d later, fed on the dead nestlings, and made further unsuccessful attempts to carry them away from the nest (Fig. 1c). At all nests where we documented cannibalism, all surviving siblings fledged in the typical fashion.

Movement of Nestlings. At two nests in the West Clare Mountains in 2010 (nests WC10a and WC10b), cameras recorded behaviors by adult females in response to movements by nestlings away from the immediate nest area (see Supplementary Material Video 2). At the first nest, a 1-d-old nestling was knocked out of the nest cup by the adult female as she left the nest. On returning, the adult female picked up and dropped the nestling twice, in what appeared to be an unsuccessful attempt at relocating it to the nest cup (Fig. 1d). The nestling made its own way back into the nest 3 min later.

At the second nest (nest WC10b), over the course of 5 d, the adult female repeatedly moved different nestlings (age 5–12 d) by picking them up or dragging them back toward the nest cup area after the nestlings had moved into the surrounding vegetation (Fig. 1e). In response, nestlings that were moved proceeded to scramble back into the vegetation. At both nests where this behavior was recorded, movement of nestlings by adults appeared to have no negative consequences for the nestlings, which continued to develop normally.

Interactions with Predators. Two nests in our study in the Ballyhoura Mountains in 2008 and 2009 (nests BM08c and BM09c, with nestlings ranging from 15–25 d old) were predated by red fox (*Vulpes vulpes*; see Supplementary Material Video 3). The first nest (nest BM08c) was unattended by either adult at time of predation. All nestlings in the nest ($n = 4$) were killed and subsequently removed from the nest area by the red fox. At the second nest (nest BM09c), the adult female was flushed from the nest by the red fox prior to predation of the full brood ($n = 2$).

At another nest in the Ballyhoura Mountains (nest BM09b) where nestlings were 5 d old, we documented an interaction between an adult female Hen Harrier and a female Eurasian Kestrel (*Falco tinnunculus*; Fig. 1f). The Hen Harrier female was in attendance at the nest when the kestrel landed, and after a 40-sec fight both birds flew off the nest (and out of camera view). All nestlings in the nest ($n = 4$) survived this event, but two died from unknown causes 10 and 25 d after the attack by the kestrel, and the remaining two siblings fledged successfully.

DISCUSSION

We found 76% of Hen Harrier nests with cameras produced an average of 2.7 nestlings per successful nest prior to the young departing our cameras' fields of view. These rates are within the range reported for Hen Harriers in various areas and years in Ireland (22–80% reported nest success; 2.1–2.8 reported nestlings per successful nests; Irwin et al. 2011). However, nestling survival rates in this study were likely overestimated, as in the later stages of development nestlings moved away from the field of view of

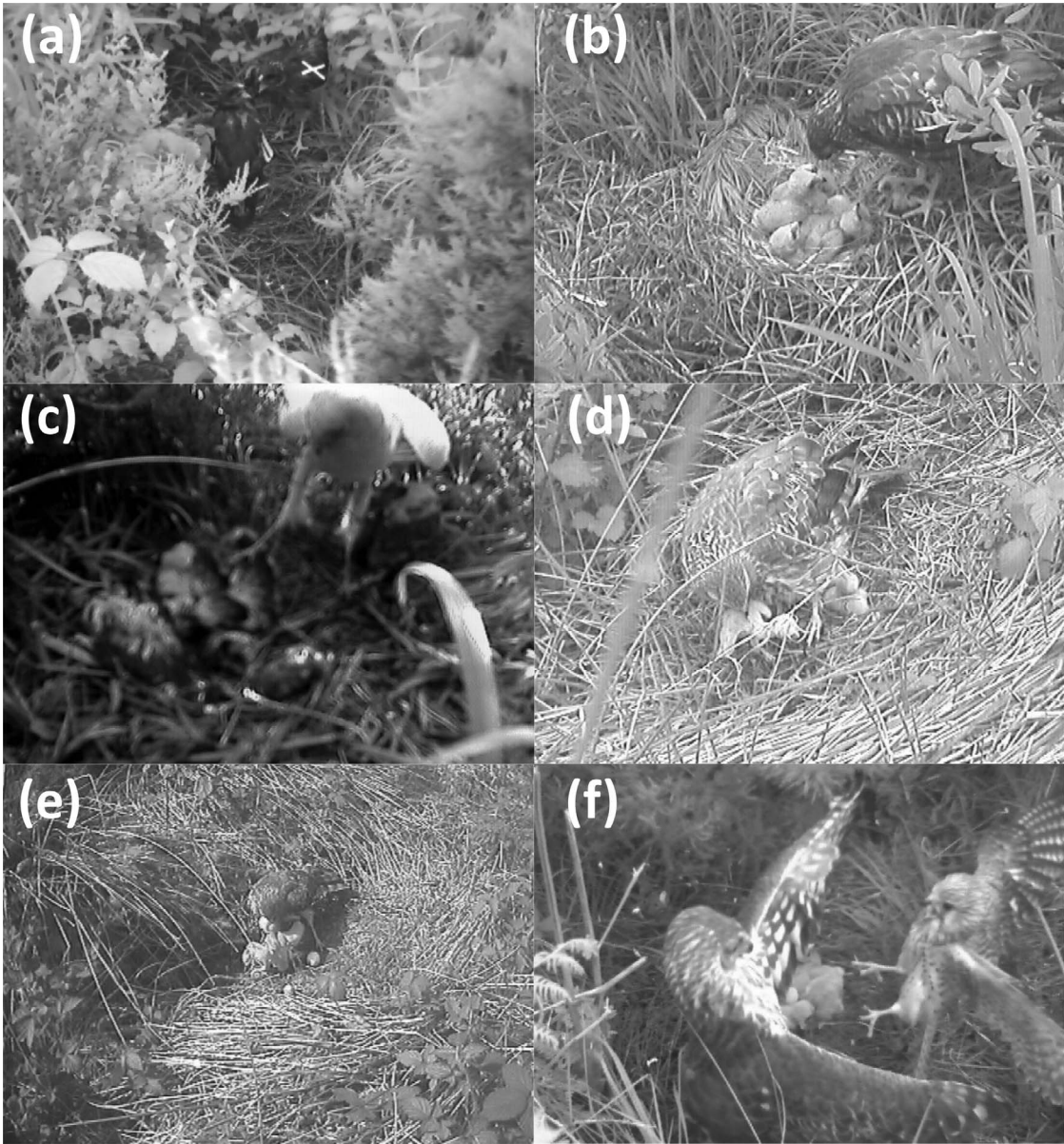


Figure 1. Behaviors recorded at Hen Harrier nests: (a) initial vocal aggression preceding siblicide at nest BM10b; (b) adult female feeding dead nestling to its siblings at nest SA10a; (c) adult male trying to carry away dead nestlings from nest BM08b; (d) female carrying newly hatched nestling at nest WC10a; (e) female carrying 10-d-old nestling at nest WC10b; (f) adult female fighting off attacking Eurasian Kestrel female at nest BM09b.

nest cameras, making it impossible to accurately determine the number of fledged young from nest-camera recordings alone.

Siblicide and Cannibalism. Many raptor species engage in siblicide (Simmons 2002, Margalida et al. 2004) and

cannibalism (Korňan and Macek 2011, Caro et al. 2014, Hadjikyriakou and Kirschel 2016). However, reports of aggression between sibling Hen Harriers are rare (Scharf and Balfour 1971, Cramp 1980), and reports of cannibalism in this species have all been assumed to involve the

consumption of nestlings that died from natural causes (Watson 1977). These reports have been based on remains found during nest visits (Balfour and Macdonald 1970, Scharf and Balfour 1971, Watson 1977) and on one occasion, on direct observations of a female flying away from the nest with a dead nestling and later returning to feed it to the remaining young (Balfour and Macdonald 1970). Our camera recordings support and augment previous reports of cannibalism in Hen Harriers. Although the sample size presented here is limited, our data suggest that this behavior is not uncommon, as some form of cannibalism was recorded at 30% of the nests included in this study. Cannibalism following the natural death of one or more nestlings is most common in raptor species with asynchronous hatching, in which younger nestlings may succumb to adverse weather or to starvation. This may be an outcome of a bet-hedging strategy, whereby brood size can be adjusted depending on food availability, with surplus nestlings that do not survive contributing to the nutritional requirements of their siblings (Watson 1977, Drummond 2001). The apparent frequency of this behavior in our study suggests that food availability may play an important role in Irish Hen Harrier populations, at least during our study period. Our study provides the first evidence of cannibalism by adult males and also of aggression and siblicide in circumstances that appear to differ from many characterizations of these behaviors in the literature. Whereas facultative siblicide has typically been associated with low food availability and interpreted as a strategy to increase food supply to the remaining nestlings (Estes et al. 1999, Simmons 2002), in the case described here, the small brood size and well-developed young make this interpretation seem unlikely. Our camera recordings suggest that interactions among nestlings in Hen Harrier broods are more complicated than previously described, and may be influenced by multiple factors, perhaps including nestling age, parental experience, food availability, or weather events. Further research will be necessary to elucidate the biological significance and frequency of these events, as well as their implications for population dynamics.

Movement of Nestlings. Our documentation of nestling moving by adult Hen Harrier females may be an interesting example of a vestigial behavior. Although it may seem to have little adaptive purpose in a ground-nesting species such as the Hen Harrier, whose nests lack any elaborate structure beyond a nest cup formed by vegetation (Watson 1977), the behavior would have had a more adaptive function in the tree-nesting ancestors of this species. Such behavior may originally have had a role in preventing nestlings from falling out of nests, retrieving fallen nestlings, or relocating nestlings from collapsed nests, as described by Robinson et al. (2017).

Interactions with Predators. As ground-nesting birds, Hen Harriers are particularly vulnerable to egg and nestling predation by mammalian and avian predators. Previous research on predation rates indicates that these vary according to region, habitat, predator species

composition, and land management, with reported rates of Hen Harrier nest predation ranging from 4% to 31% (Picozzi 1984, Etheridge et al. 1997). In Ireland, very little information is available on nest predation rates, although it has been suggested that these may vary among different nesting habitats used by Hen Harriers (Wilson et al. 2012). Our camera recordings showed that predation by red fox was a cause of nestling mortality in at least 15% of the Hen Harrier nests included in this study. Although based on a very small sample size, this is the first measure of predation rate on Hen Harriers in Ireland. It is possible that Hen Harrier nest-defense behavior may be insufficient to protect the nests and young from mammalian predators such as the red fox, one of the largest carnivores in Ireland and a common predator of ground-nesting birds (Grant et al. 1999). Conversely, a recording of the interaction between an adult Hen Harrier and a Eurasian Kestrel in this study suggests that Hen Harriers may be able to defend their nests from at least some avian predators (though it is unclear whether the target of the attack was the adult female harrier or her brood). To the best of our knowledge, this is the first description of such an interaction between a Hen Harrier and a Eurasian Kestrel. Although there are other predatory birds in Ireland, kestrels and similarly sized Carrion Crows (*Corvus corone*) are the largest that frequently predate ground nests (Grant et al. 1999). Research on Northern Harriers (*Circus hudsonius*) suggests that the main defense strategy against mammalian predators relies on selection of nest sites that are difficult for ground-based predators to access, whereas defense from avian predators depends on attendance and aggressive behaviors by adult Hen Harriers (Simmons and Smith 1985). Given the ongoing changes to Hen Harrier habitats in Ireland (Wilson et al. 2012), further research will be necessary to better understand the interactions of predators and harriers.

Conclusion. This study presents the first report of siblicide in Hen Harriers and provides further insight into cannibalistic behaviors and the birds involved (paternal and sibling cannibalism). Nest-camera recordings also yielded information on predation events and interactions with predators. Further research will be necessary to determine the importance of these behaviors in the context of reproductive rates and their consequences at a population scale.

SUPPLEMENTAL MATERIAL (AVAILABLE ONLINE)

Video 1: Recording of siblicide and cannibalism in Hen Harriers.

Video 2: Recording of nestlings being moved by adult Hen Harriers.

Video 3: Recording of nesting Hen Harrier interactions with predators.

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